

ECOLOGY AND ECOPHYSIOLOGY OF A SUBALPINE FELLFIELD COMMUNITY ON MOUNT PINOS, SOUTHERN CALIFORNIA

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ABSTRACT

Mount Pinos at the western margin of the Transverse Ranges of Southern California, reaches 2692 m in elevation at its peak. The broad summit of the mountain supports an area of subalpine fellfield vegetation, as well as an unusual low elevation occurrence of limber pine (*Pinus flexilis*). We describe the summit area of the mountain and characterize the community structure and ecophysiology of the fellfield community and associated pines. The fellfield community, dominated by low mats and cushions of *Eriogonum kennedyi*, *Phlox diffusa*, and *Lupinus breweri* var. *bryoides*, has a mean plant cover of 44%. These fellfield species have amphistomatic leaves with abundant, slender palisade cells on both sides of the mesophyll. These traits represent a strategy shared with desert plants. Amphistomaty helps to increase assimilation by maximizing stomatal conductance to CO₂ during the gas phase of diffusion, and the isolateral mesophyll maximizes diffusion of CO₂ by exposing a very high mesophyll membrane area per leaf surface area. However, the mean maximum rates of assimilation measured for *Phlox diffusa*, *Eriogonum kennedyi*, *Astragalus purshii* var. *tinctus*, and *Lupinus breweri* var. *bryoides* were 6.8 to 13.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, placing them in the lower range of those measured in alpine areas of the world.

Key Words: fellfield, *Massenerhebung* effect, Mount Pinos, photosynthetic rate.

Mount Pinos, with a summit reaching 2692 m, forms the western end of the Transverse Ranges of California. The mountain holds much botanical interest because it lies at a junction between the Coast Range to the north, the Transverse Ranges to the east, the San Joaquin Valley to the northeast (Fig. 1), and with a well-developed desert community of single-leaf pinyon pine (*Pinus monophylla*) and sagebrush (*Artemisia tridentata*) on its eastern flanks. Having high elevation, its flora is strongly related to that of the Sierra Nevada but it is well isolated across the Mojave Desert from this range.

With the exception of a single community study of Jeffrey pine (*Pinus jeffreyi*) forest stands on the south slope of Mount Pinos (Vogl and Miller 1968), there have not been ecological studies of this remarkable area. Our interests have focused on two aspects of the summit area where subalpine plants occur well below their normal range of distribution. One of these is the presence of a large fellfield community of herbaceous perennial cushions and low herbs on thin granitic soil (Fig. 2a, b), while the other is the unexpected occurrence of the subalpine conifer *Pinus flexilis*. Our objectives for this study were to describe the summit area of the mountain and to characterize the community structure and ecophysiology of the fellfield community and associated pines. Species taxonomy in this paper follows Hickman (1993).

STUDY AREA

Mount Pinos along with nearby Frazier Mountain (2365 m) are prominent mountain massifs immediately south of the San Andreas fault in the western Transverse Ranges of Southern California. These mountains are separated from the west-east trending San Emigdio and Tehachapi Ranges to the northeast by the trough of the San Andreas Fault, which is responsible for the steep north slope of Mount Pinos, while the Big Pine Fault separates Frazier Mountain from Mount Pinos (Dibble 1982). Geologic maps of these features can be seen in Kellogg (2004). These mountains, which have been variously considered the southeastern corner of the California Coast Ranges and the western margin of the Transverse Ranges, are characterized by a low profile and broad (several km²), nearly flat-topped summits. Both have unusual geology resulting from the thrusting of granitic and gneissic basement rock over sedimentary rock as young as the Pliocene.

Although it was once felt that the summits of Mount Pinos and Frazier Mountain were remnants of old erosional surfaces (Dibble 1982), recent studies suggest a different tectonic history (Kellogg 2004). Crystalline rocks underlying both mountain massifs are thoroughly fractured and crushed, being thrust above easily deformable Miocene and Pliocene sandstone, mudstone, and

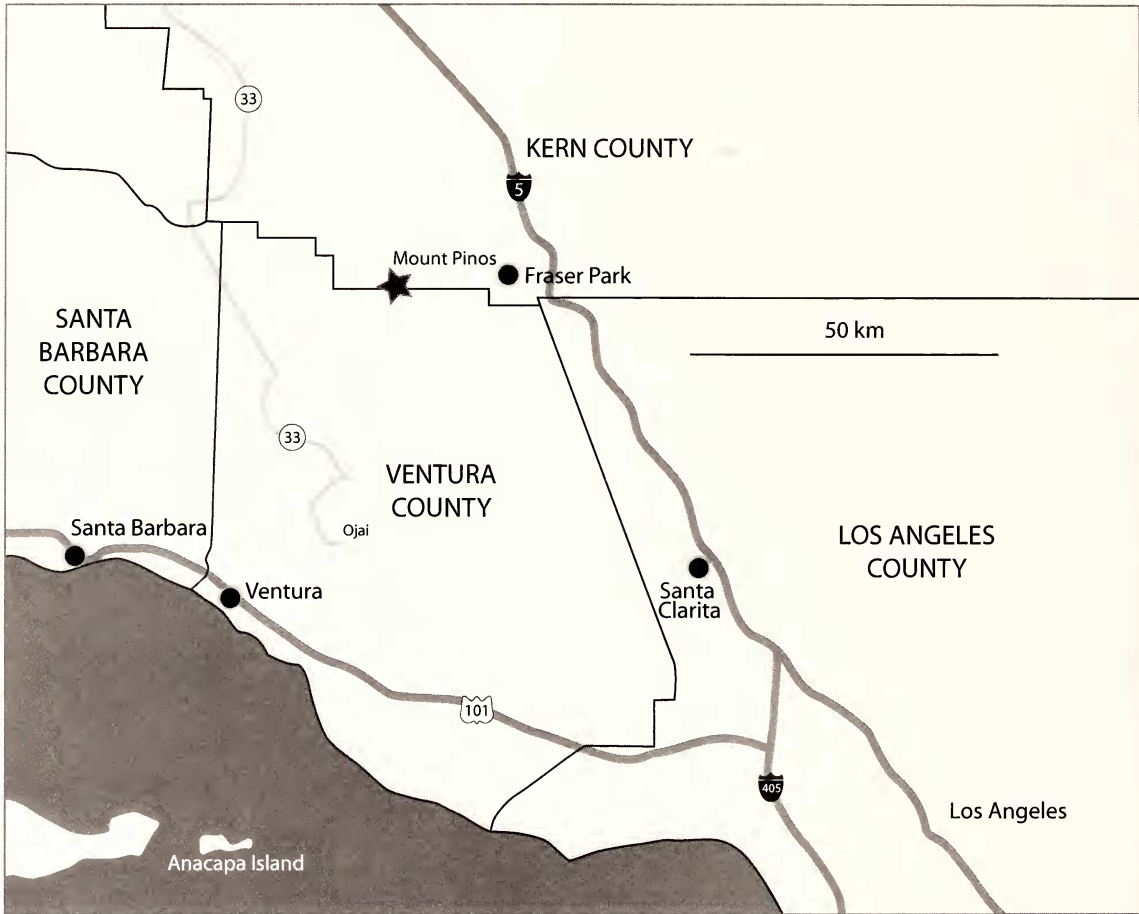


FIG. 1. Location of Mount Pinos on the western end of the Transverse Ranges on the boundary line between Ventura and Kern Counties.

shale formations below. Late Pliocene and early Quaternary thrusting associated with regional uplift and ongoing seismic activity of the San Andreas Fault have resulted in deep shattering of the granitic bedrock.

Field studies were conducted within the 206-ha Botanical Research Area comprising the broad summit area of Mount Pinos (lat. 34.48.7°N, long. 119.08.4°W) in the Los Padres National Forest. Our work was carried out in a subalpine fellfield community and adjacent open pine stands at 2650–2670 m on north- and south-facing slopes adjacent to the dirt access road to the summit. We consider this to be a subalpine community because of the fellfield community and presence of *Pinus flexilis*. The highest point of the mountain houses a U.S. Air Force microwave facility for communication between Vandenberg and Edwards Air Force Bases.

The summit area supports an open subalpine forest, with a mixed conifer community heavily dominated by Jeffrey pine (*Pinus jeffreyi*). Also present are scattered individuals of white fir

(*Abies concolor*) and single-leaf pinyon (*Pinus monophylla*). A surprising member of this conifer community is limber pine (*Pinus flexilis*), which grows along ridges in the summit area. These pines grow with an open understory of scattered low shrubs of *Ribes cereum*, *Symphoricarpos rotundifolius* var. *parishii*, and *Ceanothus cordulatus*. On other slopes with deeper soils, cushion plants commonly grow with the low shrub *Chrysothamnus viscidiflorus* subsp. *viscidiflorus*.

Several associations of fellfield community, much like typical fellfields at higher alpine locations in the Sierra Nevada, occur on the slopes where soils are thin sandy loam over fractured granite rock (Fig. 2a). These fellfield communities contain a relatively moderate diversity of herbaceous species, including cushion plants, low-growing mats, upright dicot perennials, perennial graminoids, and geophytes (Fig. 2b).

A checklist of the flora of the summit area of Mount Pinos above 2590 m includes 138 native vascular plants plus five non-native species



FIG. 2. Fellfield habitat and study species growing at about 2650 m in the summit area of Mount Pinos, California. a) General aspect of fellfield community; b) Typical cover of the fellfield community, with *Eriogonum kennedyi*, *Phlox diffusa*, and *Lupinus breweri* as dominants; c) *Astragalus purshii* var. *tinctus*; d) *Eriogonum kennedyi*; e) *Lupinus breweri* var. *bryoides*; f) *Phlox diffusa*.

(Muns 1994). The seven largest families present in this flora, excluding non-native species, are the Asteraceae (18 spp.), Scrophulariaceae (12 spp.), Fabaceae (11 spp.), Liliaceae, *sensu Jepson Manual* (9 spp.), Poaceae (8 spp.), Polemoniaceae (7 spp.), and Polygonaceae (7 spp.).

The flora is dominated by low-growing herbaceous perennials (hemicryptophytes) that annually die back to ground level. Only four tree species, as described above, and nine shrub species are present. In addition to the three shrub species listed above, shrubs present are *Chrysothamnus nauseosus*, *Holodiscus discolor*, *Ribes*

montigenum, *R. velutinum*, *Rhamnus tomentella* subsp. *cuspidata*, and *Sambucus mexicana*. The summit region is rich in geophytes, with nine species - *Iris missouriensis*, *Sisyrinchium bellum*, *Allium burlewii*, *A. campanulatum*, *A. denticulatum*, *A. fimbriatum*, *A. howellii* var. *clokeyi*, *Calochortus venustus*, *Fritillaria pinetorum*, *Muilla maritima*, and *Veratrum californicum*. Annuals are relatively abundant, with 27 native species reported.

We know of no records for precipitation for the summit area of Mount Pinos. Twisselmann (1967) suggested a mean annual precipitation of

about 430 mm, with a range from about 280 mm during a drought year to as much as 890 mm in a wet year. The USDA Forest Service Chuchupate Ranger Station, at 1603 m elevation and about 30 km by road from Mount Pinos, has a mean annual rainfall of 233 mm for a limited record of three years. North-facing slopes of the mountain hold snow well into June in wet years as in 2005, while south-facing slopes melt out far earlier. There was 1.5 to 2 m or more of snow on Mount Pinos at the end of January 2005 (Mork 2005). During dry years when snowfall is light, these summit slopes are exposed to high solar irradiance and wind for much of the year.

MATERIALS AND METHODS

Phenology

Multiple field trips to the study site in 1998 to 2005 allowed qualitative observations to be made of variable patterns of community vegetative and flowering phenology. These patterns were related to snow conditions that varied greatly between years.

Community Structure

Line transects 50 m in length along slope contours were used to sample four topographic areas of the fellfield community on June 13, 2000 to determine cover of each species, total vegetation, and exposed large rocks for each plot. Canopy interception along each transect was recorded to the nearest 5 cm for all perennial plant species. When canopies of two species overlapped, the subcanopy presence of a species was recorded separately to allow determination of total ground cover and whether any species had a characteristic understory habit. Cover of exposed large rocks (>20 cm diam.) was also measured to the nearest 5 cm along the transect.

Leaf Form and Anatomy of Cushion Plants

Anatomical characteristics of blades were first observed with a light microscope from thin transsections of several fresh leaves cut with a razor blade, and measured with an optical micrometer. Leaves were also liquid-preserved in 70% formalin-acetic acid-alcohol, dehydrated in an ethanol series, critical point dried and coated with 200 nm of gold-palladium, and then examined with an ETEC Autoscan scanning electron microscope.

Ecophysiological Characteristics

Physiological parameters of selected summit species were sampled under conditions of new growth (full leaf expansion and peak flowering),

midsummer, and fall conditions. Gas exchange measurements were made midmorning through midday on July 8, 1999, on four common cushion-forming species of the fellfield: *Eriogonum kennedyi* var. *kennedyi* (Polygonaceae), *Phlox diffusa* (Polemoniaceae), *Lupinus breweri* var. *bryoides* (Fabaceae), and *Astragalus purshii* var. *tinctus* (Fabaceae) (Fig. 2c–2f). Also measured were the photosynthetic traits of the two common pine species in the summit area, *Pinus jeffreyi* and *P. flexilis*. On November 8, 1999, we repeated these sets of measurements under late growing season conditions, but the aboveground tissues of *E. kennedyi* and *P. diffusa* were dormant on this date. Key gas exchange parameters measured were mean maximum assimilation rate (A_{\max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance to water vapor (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$), transpiration (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), and internal versus ambient CO_2 concentration ($c_i:c_a$ ratio). These measurements were obtained in situ using a LI-6200 portable photosynthesis system equipped with a 250-ml sample chamber (LI-COR, Inc., Lincoln, NB). Sample sizes on each date were typically 4–5 individuals. These measurements were made on days when the sky was cloudless, but a portable light source was used to provide saturating blue and red wavelengths of the visible spectrum (Quantum Devices, Inc. Barnsvelt, WI) at photon flux density exceeding $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PFD_{sat}) to achieve the highest possible photosynthetic rates. Maximum PFD levels at this site exceeded $2100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Reported photosynthetic rates are based on the the projected leaf area for both angiosperms and pines.

On August 5, 1999, we measured light response curves on *Astragalus purshii* var. *tinctus* and *Phlox diffusa* at the field site using the portable light source. These values were measured at ambient temperatures of 22–23°C and relative humidity of 22–25%, and VPD was 2.0–2.5 kPa. The sample chamber was covered with aluminum foil and allowed to equilibrate to obtain measurements of dark respiration.

Shoots enclosed in the sample chamber were harvested and kept in moisturized plastic bags, for determining area measured using a LI-3100 leaf area meter (LI-COR, Inc., Lincoln, NB). Manual measurements of leaf geometry were also used to verify these values. Leaves were dried for 24 hr at 85°C to determine dry weight for calculating leaf specific area (LSA, $\text{m}^2 \text{ leaf area kg}^{-1} \text{ dry leaf tissue}$).

Midday shoot water potentials of small branchlets were measured on the July and November sample dates using a Scholander-type pressure chamber (PMS Instruments). Replicate measurements were made for at least three individuals per species to calculate a mean value.

TABLE 1. PERCENT MEAN COVER OF ALL PERENNIAL SPECIES IN A SUBALPINE FELLFIELD SAMPLED ALONG PAIRS OF 25-M LINE TRANSECTS FROM FOUR REPRESENTATIVE SLOPES AT THE BOTANICAL RESEARCH AREA OF MOUNT PINOS. Line transects followed contours of the slope.

Taxa	Mean cover, %			
	Upper slope, SW-facing, slope 10%	Lower slope, SW-facing, slope <5%	Upper slope, NW-facing slope 5–10%	Upper slope, S to SE-facing, slope 10%
<i>Astragalus purshii</i> var. <i>tinctus</i>	0.2	0.0	0.0	0.6
<i>Astragalus whitneyi</i>	0.1	0.0	0.0	0.0
<i>Castilleja applegatei</i> subsp. <i>martini</i>	6.1	0.7	0.2	3.0
<i>Chrysothamnus viscidiflorus</i>	2.1	10.5	3.2	3.0
<i>Eriogonum kennedyi</i>	22.8	17.9	9.1	19.0
<i>Ivesia santolinoides</i>	0.0	0.1	1.4	0.2
<i>Leptodactylon pungens</i>	0.1	0.2	0.0	0.8
<i>Lupinus breweri</i> var. <i>bryoides</i>	0.0	0.0	8.9	0.0
<i>Lupinus lepidus</i> var. <i>confertus</i>	3.0	0.3	0.0	0.0
<i>Pedicularis semibarbata</i>	0.2	1.0	1.7	0.7
<i>Penstemon speciosus</i>	0.0	0.2	0.6	0.1
<i>Phlox diffusa</i>	5.0	15.0	12.5	7.1
<i>Silene bernardina</i>	1.6	1.7	0.8	1.2
Poaceae	2.5	2.8	3.7	1.7
Other Asteraceae	0.2	0.5	0.1	0.5
Alliaceae	0.2	0.3	0.3	0.3
Overlap, %	2.9	4.4	3.8	2.2
Total plant cover, %	41.2	46.8	38.7	37.1
Exposed rocks, %	6.5	2.3	3.3	1.8

RESULTS

Phenology

Variable snowfall conditions strongly impact the phenology of herbaceous perennials and subshrubs at the summit area. In the spring of 1998, although regional precipitation was below average, snowbanks nevertheless persisted in the pine forests adjacent to the study site into early July. At the same site in 2000, the summit received little winter snow and the study site was much drier in early July. Spring growth of the fellfield perennials and the neighboring woody shrubs *Ribes cereum* and *Chrysothamnus viscidiflorus* had begun by mid-April in 1999 and 2000, when midday air temperatures at the site characteristically reach or exceed 15°C. With the heavy snowfall of 2005, new growth of fellfield perennials and leafing of shrubs at the beginning of June was limited to warmer exposed south-facing slopes, and was there only just beginning. Flowering peaked in late July 2005.

Community Structure

Mean line transect cover of the subalpine fellfield vegetation varied from 39–51% of ground area with a mean for the four plots of 44%, whereas exposed large rocks were relatively infrequent on the four slopes (Table 1). Approximately half of the exposed ground area was soil, a sandy loam with subsurface rocks and scattered gravel on the surface. The difference between

total cover of all perennials (i.e., the sum total of canopy and subcanopy cover) and canopy ground cover in the transect measurements was only 3.2%, indicating that few individuals were growing beneath the canopies of taller plants.

Sampled vegetation, including 20 species of sampled perennial plants, was largely less than 10 cm in height. The gray-white evergreen cushion plant *Eriogonum kennedyi* had the highest cover, a mean of 17.2%. It comprised half the cover in plots 1 and 4. Plants of *E. kennedyi*, which often were present next to exposed large rocks, were typically 2–5 cm tall, and the largest mounds were up to 50 cm across.

The bright green cushion plant *Phlox diffusa* was also common and a codominant in plots 2 and 3 (Table 1). It was 2–8 cm tall, and large individuals were 30–40 cm across. The silvery-leaved, low cushion *Lupinus breweri* was common in only plot 3 and the bluish gray cushion *Astragalus purshii* was encountered only infrequently. Low shrubs (<10–15 cm in height) of *Chrysothamnus viscidiflorus* were present but widely scattered in the fellfield plots, whereas fairly dense and much taller stands of this species occurred on adjacent slopes in deeper soils. Erect herbs, such as *Silene bernardina*, the hemiparasites *Castilleja applegatei* subsp. *martinii* and *Pedicularis semibarbata*, *Penstemon speciosus*, and perennial grasses (e.g., *Elymus elymoides* and *Poa* spp.) were often encountered on the slopes but comprised very low total cover. Perennial grasses sometimes appeared to use *Eriogonum kennedyi* as a nurse plant, and *Ivesia*



FIG. 3. SEM photograph of the leaf trans-section of *Lupinus breweri* var. *bryoides*, illustrating the typical amphistomatic structure with isolateral mesophyll layers. The bar indicates 200 μm .

santolinoides with a basal rosette of leaves also commonly occurred on the edges of *Eriogonum* cushions. Geophytes (*Allium* species and *Calochortus venustus*) were emerging from bare soil patches, but individuals were less common in June 2000 than were observed in early summer 1999 and July 2005 when these geophytes were abundant.

Leaf Form and Anatomy of Cushion Plants

Leaf blades of the cushion plants were very small, and mean blade area for the four species ranged from 4.2 to 13.6 mm^2 . Blades of *Phlox diffusa* were dark green, linear and somewhat needle-like with an acicular tip, and possessed widely spaced uniseriate trichomes, which were most conspicuous on the adaxial surfaces. In contrast, leaves of *Eriogonum kennedyi* had more vertically oriented, elliptic blades that were covered with whitish vestiture, consisting of twisted unicellular trichomes, and the blade was

often enrolled somewhat to the underside. The lanceolate or narrowly ovate to elliptic leaflets of the two leguminous cushion plants, *Lupinus breweri* (palmately compound) and *Astragalus purshii* (pinnately compound), were folded along the midvein and cupped upward. Although the canopy of *L. breweri* appeared very reflectant, the adaxial blade surface was green because the reflectivity was caused by the long, straight, dense abaxial trichomes. In contrast, the leaflets of *A. purshii* were uniformly covered with softer, straight unicellular trichomes on both adaxial and abaxial surfaces.

All four cushion plant species had amphistomatic leaves with isolateral organization of the mesophyll, and each possessed at least two layers of abaxial palisade chlorenchyma (Fig. 3, Table 2). Mean blade thickness ranged from 209 μm in *E. kennedyi* to 497 μm in the thicker but extremely narrow leaf of *P. diffusa*. Primary phloem fibers were present in midveins of all species, but in addition *P. diffusa* had a zone of

TABLE 2. LEAF ANATOMICAL AND MORPHOLOGICAL TRAITS OF EIGHT COMMON FELLFIELD PERENNIALS FROM THE SUMMIT AREA OF MOUNT PINOS. ND = no data collected.

	Leaf thickness (μm)	Stomatal form	Mesophyll	Leaf specific area ($\text{m}^2 \text{kg}^{-1}$)
<i>Astragalus purshii</i> var. <i>tinctus</i>	227	amphistomatic	isolateral	92.5
<i>Castilleja applegatei</i>	270–442	amphistomatic	isolateral	ND
<i>Eriogonum kennedyi</i>	209	amphistomatic	isolateral	40.5
<i>Lupinus breweri</i> var. <i>bryoides</i>	298	amphistomatic	isolateral	70.9
<i>Pedicularis speciosus</i>	1728	amphistomatic	isolateral	ND
<i>Penstemon speciosus</i>	432	amphistomatic	isolateral	ND
<i>Phlox diffusa</i>	497	amphistomatic	isolateral	62.1
<i>Silene bernadina</i>	583	amphistomatic	isolateral	ND

fibers along the two leaf margins and the fibrous leaf apex was produced as an extension of the midvein fiber. These fibers were highly developed and contributed greatly to leaf thickness. Moreover, leaves of *P. diffusa* become somewhat spine-like when they senesce.

Leaf specific area (LSA) was high for leaflets of *A. purshii* ($92.5 \text{ m}^2 \text{ kg}^{-1}$). Means of LSA were very slightly lower for *L. breweri* ($70.9 \text{ m}^2 \text{ kg}^{-1}$) and *P. diffusa* ($62.1 \text{ m}^2 \text{ kg}^{-1}$), while the leaves of *E. kennedyi* had the lowest LSA ($40.5 \text{ m}^2 \text{ kg}^{-1}$). In comparison, pines, with a very different anatomical structure, had low LSA values of 28.5 and $24.1 \text{ m}^2 \text{ kg}^{-1}$ for *Pinus flexilis* and *P. jeffreyi*, respectively.

Ecophysiological Characteristics

In early July 1999, the two legume species, *A. purshii* and *L. breweri*, had assimilation rates (A_{max}) of 13.4 and $13.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (Table 3). Stomatal conductance (g_s) was 293 and $263 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the two species. *Phlox diffusa* had a relatively low A_{max} of $6.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, but proportionally high value of $212 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for g_s . *Eriogonum kennedyi* had an assimilation rate of $8.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, but a low g_s rate of $74 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Higher values of $A:E$ and $A:g_s$ and lower values of $c_i:c_a$ ratio indicate higher water-use efficiency. *Eriogonum kennedyi* demonstrated the highest water-use efficiency by all three of these measures (Table 3).

In early November 1999, the aboveground tissues of both *P. diffusa* and *E. kennedyi* as well as many other species were no longer active. Two other two fellfield cushion plants had positive but low rates of assimilation. *Astragalus purshii* had an assimilation rate of $3.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 28% of its July rate, while *Lupinus breweri* with an assimilation rate of $5.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was at 36% of its July level.

For the two pine species in early July, *P. jeffreyi* was the most active with an assimilation rate of $11.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 3). Photosynthesis was also moderately high in *P. flexilis* with a rate of $8.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. There was little change in these rates four months later in early November. *Pinus jeffreyi* had an assimilation rate of 91% of its July rate while *P. flexilis* was at 96% of its previous rate (Table 3). Water-use efficiency did not increase significantly over this seasonal period in the pines. Overall, the water-use efficiencies by all three measures were significantly higher on both dates in the pines than in three of the four fellfield cushions. Only *E. kennedyi* had a broadly comparable level of water-use efficiency (Table 3).

Light response curves measured in early August 1999 showed that *P. diffusa* and *A. purshii* both achieved light saturation for photo-

synthesis at high levels of about $1500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Fig. 4a,b). At PFD_{sat} , A_{max} for the silvery leaves of *A. purshii* was $18.71 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when g_s was $189 \text{ mmol m}^{-2} \text{ s}^{-1}$, whereas A_{max} of the bright green, fibrous leaves of *P. diffusa* was only $6.54 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when g_s was $110 \text{ mmol m}^{-2} \text{ s}^{-1}$.

Xylem water potentials of the two fellfield legumes, *A. purshii* and *L. breweri*, dropped to lower levels (higher water stress) between the July and November sample dates (Fig. 5). *Eriogonum kennedyi* maintained relatively constant water potentials of about -2.5 MPa over the two sample dates. *Phlox diffusa* (not photosynthetically active in November) and the two pine species showed a reverse pattern of higher water potentials (lower water stress) in November.

DISCUSSION

Although the flora of the summit area of Mount Pinos is strongly Sierra Nevada in its flora (Muns 1994), this massif has been climatically isolated from the Sierra Nevada since the Pleistocene. Moreover, the current climate regime of Mount Pinos makes the summit region much more seasonal in climate and more arid than comparable sites in the Sierra Nevada. This isolation and relative aridity can be seen in the presence of distinct subspecies and a number of desert elements. Examples of these are non-Sierran taxa such as *Eriogonum kennedyi* var. *kennedyi*, *Phacelia mohavensis*, *Allium howellii* var. *clokeyi* (a local endemic), *Castilleja applegatei* subsp. *martini*, and *Astragalus whitneyi* var. *whitneyi*.

The presence *Pinus flexilis* on Mount Pinos is unexpected based on its typical habitat distribution. Whereas this species also can be found in small numbers on nearby Brush Mountain to the northwest of Mount Pinos and Frazier Peak to the east (Twisselman 1967), the nearest populations to these occur at high elevations 130 km to the east in the San Gabriel Mountains of the Transverse Ranges (Thorne 1977). *Pinus flexilis* does occasionally occur as low as 2560 m in the higher Transverse and Peninsular Ranges, but is more typical of higher elevations of 2750 to 3300 m . Although the rainfall at the summit of Mount Pinos is far lower than that of comparable sites with *P. flexilis* in the Sierra Nevada and in the high Transverse and Peninsular Ranges, it is similar to that present in the White Mountains of California where *P. flexilis* and *P. monophylla* can be found growing in close proximity at about 3050 m elevation (Rundel, personal observation).

Pinus contorta subsp. *murrayana* (lodgepole pine), commonly associated with *P. flexilis* in the Sierra Nevada and higher Transverse and Peninsular Ranges, is absent from Mount Pinos. Two

TABLE 3. PHYSIOLOGICAL CHARACTERISTICS FOR FOUR SPECIES OF CUSHION PLANTS AND TWO PINE SPECIES MEASURED ON JULY 8, 1999 DURING PEAK FLOWERING AND ACTIVE VEGETATIVE GROWTH, AND NOVEMBER 5, 1999 ENTERING WINTER DORMANCY, AT 2630–2670 M IN A SUBALPINE FELLFIELD AND NEAR THE SUMMIT OF MOUNT PINOS. Ambient conditions of full sun and cloudless sky, vapor pressure deficit 2.2 kPa, essentially no wind; July 8 ambient temperature was 27–31°C with 40–44% relative humidity; November 5 ambient temperature was 16–18°C with 10–12% relative humidity. Mean maximum assimilation rate at saturated PFD (A_{\max}), stomatal conductance (g_s), transpiration rate (E), instantaneous water-use efficiency ($A:E$), intrinsic water-use efficiency ($A:g_s$ and $c_i:c_a$ ratio). Means \pm standard errors are shown in parentheses after each value.

Species	A_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	g_s ($\text{mmol m}^{-2} \text{ s}^{-1}$)	E ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	$A:E$	$A:g_s$	$c_i:c_a$ ratio
<i>Astragalus purshii</i> var. <i>tinctus</i>						
8 July	13.35 (± 0.85)	293 (± 22)	10.53 (± 0.83)	1.28 (± 0.06)	46 (± 3)	0.685 (± 0.015)
5 November	3.79 (± 0.58)	62 (± 0.7)	1.78 (± 0.19)	2.22 (± 0.33)	64 (± 10)	0.689 (± 0.052)
<i>Eriogonum kennedyi</i>						
8 July	8.23 (± 0.61)	74 (± 0.1)	3.86 (± 0.22)	2.16 (± 0.26)	111 (± 8)	0.365 (± 0.049)
<i>Lupinus breweri</i> var. <i>bryoides</i>						
8 July	13.93 (± 0.49)	263 (± 24)	7.43 (± 0.23)	1.89 (± 0.10)	55 (± 4)	0.676 (± 0.018)
5 November	5.04 (± 0.51)	124 (± 8)	2.73 (± 0.21)	1.91 (± 0.27)	41 (± 4)	0.710 (± 0.041)
<i>Phlox diffusa</i>						
8 July	6.77 (± 0.43)	212 (± 15)	6.10 (± 0.51)	1.12 (± 0.06)	32 (± 1)	0.785 (± 0.015)
<i>Pinus flexilis</i>						
8 July	8.08 (± 0.32)	90 (± 3)	3.32 (± 0.20)	2.46 (± 0.17)	90 (± 3)	0.512 (± 0.015)
5 November	7.77 (± 0.31)	64 (± 5)	1.46 (± 0.07)	5.34 (± 0.19)	122 (± 5)	0.409 (± 0.026)
<i>Pinus jeffreyi</i>						
8 July	11.32 (± 0.89)	108 (± 10)	3.88 (± 0.32)	2.93 (± 0.10)	105 (± 3)	0.387 (± 0.024)
5 November	10.29 (± 0.99)	90 (± 3)	2.68 (± 0.30)	3.86 (± 0.06)	116 (± 4)	0.409 (± 0.037)

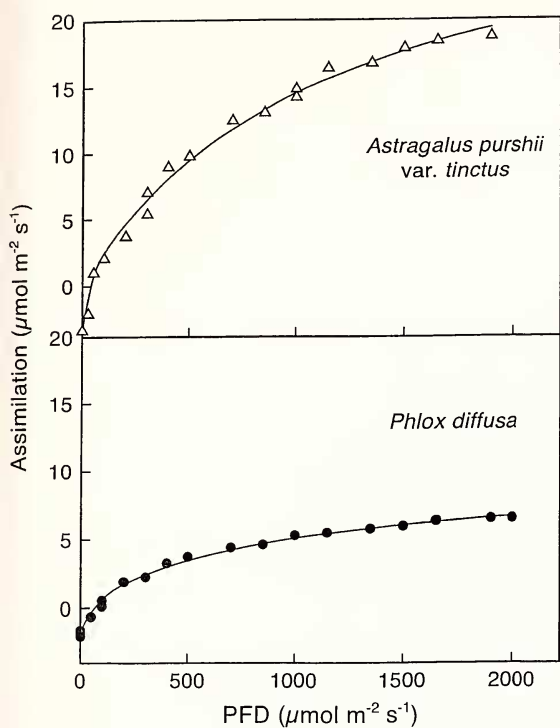


FIG. 4. Light response curves of net photosynthesis in relation to photon flux density (PFD) irradiance for *P. diffusa* and *A. purshii* var. *tinctus*.

common montane conifers from the Sierra Nevada and higher Transverse Ranges, *Pinus lambertiana* (sugar pine) and *Calocedrus decurrens* (incense cedar), are present but limited to isolated local populations on Mount Pinos despite the apparent presence of appropriate habitats.

The rates of assimilation measured for the four fellfield species on Mount Pinos were in the lower portion of the range of those measured in alpine areas in other parts of the world (Körner 1999). These values ranged from 6.8 to 13.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ on Mount Pinos, can be compared with a range of 11.5 to 25.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ reported for eight fellfield species in the arid White Mountains of California (Rundel et al. 2005). With the exception of *Eriogonum kennedyi*, which had a very low value of $c_i:c_a$ ratio in our study, White Mountain species generally had lower values of $c_i:c_a$ ratio than those reported here for Mount Pinos, indicating higher water-use efficiency. The assimilation rates and stomatal conductances of the two pine species on Mount Pinos fall within the ranges of values previously reported for pines in the literature (Rundel and Yoder 1998).

The November measurements of water potential showed an expected decrease in water potential from July values for *Astragalus purshii* and *Lupinus breweri* following dry summer

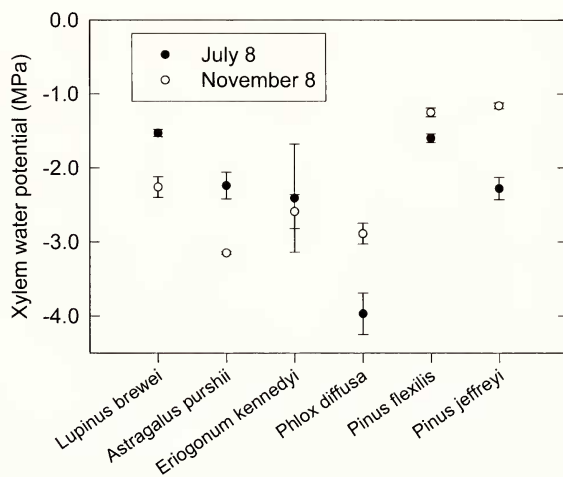


FIG. 5. Midday xylem water potential on July 8, and November 8, 2005, for *Lupinus breweri* var. *bryoides*, *Astragalus purshii* var. *tinctus*, *Eriogonum Kennedyi*, *Phlox diffusa*, *Pinus flexilis*, and *P. jeffreyi* in the summit study site at 2650 m on Mount Pinos.

conditions. Water potential, however, remained relatively constant in *Eriogonum kennedyi* and increased in *Phlox diffusa* and the two pine species. Both *E. kennedyi* and *P. diffusa* were dormant in November and thus an absence of transpiration reduced water stress. We do not have sufficient data to fully interpret the reduced water stress in the pine species at a time when photosynthetic rates were not significantly different from July rates, but this likely relates to cooler temperatures in November that reduced transpirational water loss and increased water-use efficiency as seen in ratios of assimilation to transpiration.

Many accounts of California plant life have noted that numerous genera present on mountaintops also have congeners occurring in lowland deserts (Went 1948), and so desert-alpine comparisons should also be considered. Like nonsucculent dicotyledons of the nearby Mojave Desert (Rundel and Gibson 1996), the four fellfield species used for gas exchange measurements have leptophylls, i.e. minute leaves or leaflet blades. For desert plants, such microphyllous leaves have the adaptive benefit of staying close to ambient temperature, hence never reaching lethal high temperatures, because such leaves have thin boundary layers and high conductive heat exchange (Gibson 1996, 1998; Smith et al. 1997). At alpine and subalpine elevations, such leaves that track cool daytime temperatures would be below expected optimal temperatures for photosynthesis. Although cushion plants with full sun exposure throughout the day never experience high air temperature, the cushion canopy may become heated via radiation and conduction from warm soil surfaces and thus have leaf temperatures substantially above air

temperatures. Temperatures of low, ground hugging dense mats can be 20°C or more above air temperature (Körner 1999; Rundel et al. 2005). Many such mats and cushions have densely packed leaves, making the operational boundary layer for gas exchange that of the canopy itself rather than individual leaves.

Fellfield plant species on Mount Pinos have amphistomatic leaves with abundant, slender palisade cells on both side of the mesophyll. These traits appear to be those present in many desert plants worldwide (Gibson 1996, 1998). Amphistomaty helps by increasing instantaneous rates of assimilation by maximizing stomatal conductance to CO₂ during the gas phase of diffusion (Mott et al. 1982), and isolateral mesophyll tends to maximize diffusion of CO₂ in liquid phase by exposing a very high mesophyll cell membrane area per leaf surface area (Nobel 2005). When leaves are not severely water stressed (e.g. midmorning during weeks of peak growth under saturated PFD), maximal instantaneous assimilation rates of desert annuals and perennials often reach or exceed 25 μmol CO₂ m⁻² s⁻¹ (Gibson 1998), levels generally higher than those reported for alpine fell field species (Rundel et al. 2005). Critical studies are needed to determine why desert plants have higher assimilation rates than related alpine plant species, and also how congeners from the two habitats may differ in allocation of photosynthate to vegetative and reproductive growth, and to tissue maintenance.

The causal factors explaining the relatively low elevation occurrence of subalpine fellfield and limber pine forest communities on Mount Pinos remain an open question for investigation. Fellfield plant communities are generally found on high elevation sites near or above treeline. These sites are typically exposed and dry, often windy and snow-free summits and ridges where snowmelt occurs rapidly and wet soils do not persist (Bliss 1985). Subalpine fellfield and treeline conifers rarely occur as low as 2800 m in the southern Sierra Nevada but are more characteristic of elevations well above 3500 m. The summit of Mount Pinos may well have these traits in most winters because of the relatively low amounts of snowfall and the exposed position of the mountain near the coast. However, in cold and wet winters, snowfall covers much of the summit area through the late spring into early summer, as occurred in 2005.

One component of an explanation for the subalpine communities of Mount Pinos lies with the *Massenerhebung*, or mass-elevation, effect, which has been documented for the Alps of Central Europe (Barry 1982). Core areas of the central Alps have a higher elevation treeline than those present on peaks at the outer margins of the range. Greater solar radiation inputs in these core

areas have been hypothesized to lead to warmer summer temperatures with reduced duration of snowfields, and thus longer growing seasons. This effect also predicts lower elevation treelines on isolated mountains compared with elevations on larger mountain ranges with greater mass. The summit of Mount Pinos is relatively isolated and sufficiently close to the coast to be influenced by maritime conditions and cloud cover, moderating solar radiation and temperatures at the summit. Moreover, growing season length likely is also reduced by the extreme summer aridity on Mount Pinos. Thus, moderate summer temperatures and drought-shortened growing season conditions would act to lower timberline. As noted above, scattered individuals of *Pinus flexilis* do occur at similar elevations in the San Gabriel, San Bernardino, and San Jacinto Mountains, but the primary range of the species in these ranges is above 2750 m. Detailed climatological measurements on the summit of Mount Pinos could help resolve this interesting issue.

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